THE FEEDING BEHAVIOR AND RESPIRATION OF SOME MARINE PLANKTONIC CRUSTACEA [1]

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Interest in the respiratory rate and food requirements of the marine zooplankton probably dates from the studies of Pütter (1907, 1909), but data are presently available for only a dozen or so species of neritic copepods and for *Euphausia pacifica* (Lasker, 1960). *Paraeuchaeta norvegica,* studied by Raymont and Gauld (1951), is the only marine copepod for which respiratory measurements are available, which commonly occurs at depths greater than 100 meters.

In the present work a number of shipboard and laboratory experiments were performed with oceanic species of copepods, amphipods and euphausids, some from deep water, to learn if such organisms were amenable to artificially controlled conditions, and to obtain additional respiratory data for a very important but little-studied group of animals. A few species previously investigated from other localities (*i.e., Calanus finmarchicus*) were also included for comparative purposes.

In addition to the respiratory measurements, representatives of most species investigated were also kept in laboratory culture vessels where observations were made on their behavior and food habits. Some individuals of the copepod, *Calanus hyperboreus,* have been maintained in the laboratory for approximately one year which would seem to be the life span for it. Because of its large size, long life span, and ability to adapt to laboratory conditions, this species is currently the subject of intensive experimental investigation.

The author would like to express his appreciation to Dr. G. L. Clarke, Dr. Herbert Curl, Michael Mullin, William Dawson, Henry Fuller, John Clarke, Thomas Renshaw and Masateru Anraku, all of whom gave field or laboratory assistance during different phases of the work reported here. Dr. Robert Guillard supplied the phytoplankton cultures and Dr. Rudolf Scheltema supplied *Artemia* eggs and certain planktonic larvae used in feeding experiments. Dr. Robert Hessler supplied the *Artemia* used in the respiratory experiments.

Materials and Methods

The zooplankton organisms used in the present program included the copepods: *Calanus finmarchicus, C. hyperboreus, Paraeuchaeta norvegica, Pleuromamma robusta, Bathycalanus* sp., *Rhincalanus nasutus, Euchirella rostrata;* the amphipods *Phronima* sp., *Euthemisto compressa,* and *Hyperia galba,* and an unidentified euphausid probably belonging to the genus *Thysanoessa.* All these animals are of

[1] Contribution No. 1115 from the Woods Hole Oceanographic Institution. This research was supported by the National Science Foundation under Research Grants 3838, 8913 and 8339.

large size and easily recognizable with the naked eye, even on shipboard. For the graphic analyses of respiratory rates use was also made of some data, hitherto unpublished in the present form, for the small neritic copepod *Acartia clausi*.

The animals were captured with a ¾-meter or 1-meter net of mesh size #00 or #000, with a glass jar of one quart capacity secured in the cod-end. Tows were generally 15 to 30 minutes at depth, but in the case of the deeper tows the time required to reach the desired depth and to recover the net again increased the total towing time appreciably. Before the net was brought aboard after fishing, care was

TABLE I

Summary of all experimental data on the respiratory rates of zooplankton

Copepods	Location of experimental tow and estimated depth	Date	No. & stage	Experimental temp. ° C.	Dry weight/animal mg.	Respiration rate:	
						µl./animal & day	µl./mg. dry wt.& day
Calanus finmarchicus	Georges Bank 41°00′ N 67°35′ W 25 m.	Aug. 18, 1958 Aug. 18, 1958 Aug. 18, 1958 Aug. 18, 1958 Aug. 18, 1958 Aug. 18, 1958 Aug. 18, 1958 Aug. 18, 1958 Aug. 18, 1958	4 V 4 V 15 V 4 ♀ 15 ♀ 4 V 4 V 15 V 4 ♀*	7.5 7.5 7.5 7.5 7.5 18.5 18.5 18.5 18.5	0.188 0.188 0.232 0.211 0.214 0.188 0.188 0.199 0.211	4.4 5.4 5.5 9.5 9.0 9.0 8.9 8.7 15.7	23.0 28.8 23.3 44.1 42.0 47.3 51.9 42.0 74.2
Calanus finmarchicus	Gulf of Maine 42°25′ N 69°47′ W 200 m.	Aug. 20, 1958 Aug. 20, 1958 Aug. 20, 1958 Aug. 20, 1958 Aug. 20, 1958	15 V 15 V 15 V 4 V 4 V	8 8 8 8 8	0.294 0.264 0.334 0.277 0.277	4.7 3.9 3.6 5.4 4.7	16.2 14.8 10.9 19.5 16.9
Calanus hyperboreus	Slope water 41°46′ N 65°28′ W 1000 m.	Aug. 19, 1958	7 V 5 ♀ 1 ♀	<10 <10 <10	1.55 3.68 3.62	18.3 24.8 26.0	11.8 5.5 7.1
Paraeuchaeta norvegica	Slope water 41°46′ N 65°28′ W 1000 m.	Aug. 19, 1958	5 ♀ 5 ♀ 1 ♀	<10 <10 <10	3.88 3.80 4.59	47.6 51.5 48.7	12.2 13.8 10.5
Pleuromamma robusta	Slope water 38°28′ N 70°59′ W 450 m.	Aug. 15, 1958	3 ♀ 3 ♀	8 8	0.283 0.283	19.0 15.5	66.5 54.3
Bathycalanus sp.	Slope water 41°46′ N 65°28′ W 1000 m.	Aug. 19, 1958	1 ♀	5.1	17.9	163.4	9.1

* 3 animals died.

TABLE I—*Continued*

Copepods	Location of experimental tow and estimated depth	Date	No. & stage	Experimental temp. ° C.	Dry weight/animal mg.	Respiration rate:	
						µl./animal & day	µl./mg. dry wt. & day
Rhincalanus nasutus	Slope water 39°48′ N 71°12′ W 400 m.	April 22, 1959	2 ♀ 2 ♀ 2 ♀	6.5 6.5 6.5	0.826 1.079 1.019	13.0 15.3 15.0	15.7 14.2 14.7
Euchirella rostrata	Slope water 39°48′ N 71°12′ W 400 m.	April 22, 1959	3 ♀ 3 ♀ 3 ♀	6.5 6.5 6.5	0.890 0.947 0.820	22.4 28.6 25.6	25.2 34.9 27.0
Acartia clausi	Long Island Sound 5–10 m.	July 22, 1953 Jan. 6, 1954 Jan. 26, 1954 Feb. 2, 1954 July 3, 1954 July 10, 1954	119 ♀ 47 ♀ 156 ♀ 49 ♀ 100 ♀ 52 ♀	5.0 5.0 5.6 5.0 5.9 5.9	0.0041 0.0047 0.0073 0.0072 0.0044 0.0049	0.30 0.37 0.67 0.69 0.40 0.22	73.1 78.7 91.8 95.8 90.9 42.6
Euphausids (unidentified)	Slope water 41°46′ N 65°28′ W 1000 m.	Aug. 19, 1958	3 ** 1	5.1 5.1	2.67 3.39	43.1 105.7	16.1 31.0
Amphipods *Phronima* sp.	Slope water 38°28′ N 70°59′ W 450 m.	Aug. 15, 1958	1	8	27.3	284.9	10.4
Euthemisto compressa	Gulf of Maine 42°25′ N 69°47′ W 200 m.	Aug. 20, 1958	4 4 4	4 4 4	4.97 4.87 4.35	92.7 87.5 72.3	18.6 18.0 16.6
Hyperia galba	Gulf of Maine 42°35′ N 69°35′ W 250 m.	Dec. 4, 1959	1 1 1 1	5.6 5.6 5.6 5.6	3.52 8.24 4.62 10.15	51.2 81.0 70.7 114.2	14.5 9.8 15.3 11.2

** 1 animal in poor condition.

taken to have on hand fresh sea water pre-cooled to a temperature at or near that of the depth fished. The cod-end was immersed in this water and the contents of the glass jar only were retained. It was assumed that animals crushed against the meshes of the net were likely to be damaged, so that the net was never washed down and the entire process of getting the organisms from their natural temperature conditions to conditions simulating them was carried out as rapidly as possible. If the temperature difference between the surface water and the depth fished was great,

the mortality among the deep-water forms was high despite the precautions taken. However, the animals were sorted immediately and only the healthy specimens kept for experimental work.

On shipboard, a portable refrigerator which opened from the top was used as an experimental laboratory. In the earlier studies, some difficulty was encountered in regulating the temperature of this box when it was opened frequently. A larger expansion valve, enabling higher refrigerant pressures, eliminated this difficulty, and in its present form the box can be kept open for long periods even in summer without excessive temperature change. On return to land facilities, a constant temperature room and conventional refrigerated water baths provided supplementary, controlled-temperature conditions when required.

Since most of the animals used in this study came from water deeper than 200 meters, 5–6° C. was chosen as the temperature at which the experimental and observational studies would be run, although for reasons mentioned above this was not attained in every case (see Table I). Initially it was hoped to compare the respiration of some of the animals at 5° and at surface temperature, to enable the computation of a rough Q_{10}. However, prolonged exposure to warmer surface waters proved lethal to most of the experimental material so that except for the relatively eurythermal *Calanus finmarchicus,* such a comparative study was not possible.

Respiration was measured using glass-stoppered bottles of appropriate size. Animals were placed in a small quantity of water in a bottle, and then the bottle and contents were flushed several times with water of known oxygen content, using a siphon arrangement with a bolting cloth screen to prevent loss of the experimental material. Control bottles were prepared in precisely the same manner except that the animals were omitted. All bottles were filled completely, taking care to insure that no air bubbles were included. As Marshall *et al.* (1935) demonstrated an increase in respiration for *Calanus finmarchicus* on exposure to light, all bottles were placed in black cloth bags during the run, regardless of the experimental conditions. At the end of a suitable period of time (8 to 48 hours), single samples from the experimental and the control bottles were siphoned into smaller glass-stoppered bottles and the oxygen content determined by the Winkler method. The oxygen utilization was determined from the difference between the bottles containing animals and those without. (For a detailed description of the method, with a discussion of its advantages and disadvantages, see Conover, 1956, 1959.)

The animals themselves were generally dried for weighing while in fresh condition, or in some instances a sample of the same species and stage of animal was dried as representative of the experimental animals. Animals were weighed on a suitable quartz helix microbalance made by the Microchemical Specialties Company, Berkeley, California. In the case of the smaller organisms such as *Calanus finmarchicus* a balance with working sensitivity of 2 mg. $\pm$ 1 μg. was used. For larger forms a 20 mg. $\pm$ 10 μg. balance was employed. Aside from the accuracy of weighing in this manner, the process is extremely rapid and largely free from errors due to sudden temperature change, varying humidity, etc. In a few instances, the animals were too large for either helix and they were weighed on a conventional analytical balance.

In the respiration experiments, as well as in laboratory culture studies, antibiotics

were used to control bacterial growth and respiration. Dihydrostreptomycin sulfate in concentration 50 mg./L. was generally used in respiratory studies, sometimes supplemented with 10 mg./L. of chloromycetin. Chloromycetin was found to have an inhibitory effect on the feeding of *Calanus finmarchicus* when used at 50 mg./L. (Conover, Marshall and Orr, 1959). Since oxygen utilization attributable to bacteria was generally less than 0.1 ml./L., even in 48-hour experiments, with streptomycin alone, chloromycetin was eventually eliminated altogether from the experimental procedure.

For laboratory culture experiments, the organisms were kept in polyethylene "freezer containers" of pint, pint and a half, quart, or gallon size, depending on the size and number of animals to be cultured. These containers proved non-toxic to all animals tested, and, when fitted with their plastic tops, were safe from spillage or breakage in a rough sea. For most organisms, one or two animals in the pint-sized container proved most satisfactory; the containers then could be conveniently stacked four or five high without danger of upsetting, and in this size the sides are low enough to permit easy observation with a dissecting microscope.

Sea water for cultures was passed through a type AA Millipore filter (pore size 0.80 μ), cooled, and aerated before use. In the earlier studies, the culture water was generally taken from the same area that produced the animals, but it was found that local water from Vineyard Sound was also satisfactory. Streptomycin and penicillin "G" potassium 50 mg./L. were used together at first, but later alternated at each change of culture medium to lessen the possibility of "antibiotic resistance" developing among the contaminating bacteria.

The phytoplankton organisms tried as food for the animals included *Skeletonema costatum, Thalassiosira decipiens, T. fluviatilis, Chaetoceros affinis, Rhizosolenia setigera,* and *Coscinodiscus asteromphalus,* all from laboratory cultures. Living *Artemia* nauplii and *Pinnotheres* zoeae, fresh-caught harbor copepods including *Acartia clausi, A. tonsa, Temora longicornis, Centropages hamatus, Eurytemora hirundoides,* and *Labidocera aestiva,* as well as various invertebrate larvae in the plankton were given as animal food. Bits of mussel, clam, and living and dead offshore zooplankton were also given to some of the larger carnivorous forms. The number of fecal pellets produced was used as a criterion for the amount of feeding although in a few instances change in the number of food organisms was also determined.

No attempt was made to determine the food in nature by examination of gut contents. Food passes through the animal's gut very rapidly and particularly in the case of offshore forms the gut is usually empty.

Observations on Feeding and Behavior of Animals in the Laboratory

Copepods

Calanus finmarchicus. Marshall and Orr (1955a, 1955b) have summarized what is known concerning the feeding and behavior of this species, and little can be added by this investigation. *Calanus finmarchicus* is known to eat a wide variety of diatoms, dinoflagellates, and other flagellated forms. Nannoplankton is eaten but the animal showed a decided preference for larger food (Marshall and Orr, 1955b). In addition, radiolarians, tintinnids, and crustacean remains have been

found in the gut (Marshall and Orr, 1955a). In the present study, *C. finmarchicus* ate *Skeletonema, Rhizosolenia,* and both species of *Thalassiosira.* Although it may take in animal food inadvertently, it would seem that this species is primarily a herbivore.

Calanus hyperboreus. This species is generally regarded as an arctic form, where it commonly occurs in the surface waters. It is moderately abundant in the Gulf of Maine and has been observed in the slope water at depths greater than 400 meters as far south as about 38° N. Juveniles were captured a mile south of Gay Head on Martha's Vineyard, Massachusetts, in March and April, 1958.

When first returned to the laboratory, *C. hyperboreus* generally did not eat any plant or animal food readily, but after one to two weeks healthy specimens ate all phytoplankton species presented to them, including *Skeletonema costatum, Thalassiosira decipiens, T. fluviatilis, Chaetoceros affinis* and *Coscinodiscus asteromphalus.* Many large fecal pellets were produced, often two or three millimeters long, which on microscopic examination contained some green material and abundant smashed tests of the species of diatom fed.

This species is anatomically very similar to *C. finmarchicus* and is almost certainly herbivorous in northern seas. However, it is difficult to understand how it can obtain plant food in sufficient abundance to sustain it in the slope waters south of Woods Hole, Massachusetts, in summer when the waters of the euphotic zone are too warm for it. Possibly the animal goes into a state of "quiescence" when food is scarce, which may explain why no food is taken when it is first brought into the laboratory. Recent unpublished experiments suggest that the increase in activity after some days in the laboratory is also accompanied by an increase in respiratory rate.

Sømme (1934) observed that breeding animals frequently ate their own eggs. This observation has been confirmed in the present study, but it was found that egg-eating was much greater when animals had no other food available than when abundant phytoplankton was present.

Paraeuchaeta norvegica. Lowndes (1935) examined living and preserved specimens of this large copepod and concluded that it was entirely carnivorous. The animal refused all plant food presented to it in the current work. On the other hand, some of the laboratory specimens fed on small neritic copepods readily as long as they were alive. *Acartia tonsa* and *Centropages hamatus* were taken frequently, although it is questionable whether *Paraeuchaeta* would encounter either in nature commonly. It did not eat *Artemia,* though some decapod larvae were consumed. During feeding, fecal pellets were produced which contained obvious animal fragments. If both plant and animal material were fed simultaneously, the fecal pellets produced contained only animal remains.

The maxillipeds in this animal are large, prehensile and carried far forward in "praying mantis" fashion. The actual capture of the prey was not observed but the animal would seize the end of a needle or micropipette when irritated in a manner which must closely duplicate the process of food getting. The strength of the animal was surprising and a smaller copepod would have little chance of escape once it was grasped by the maxillipeds. Curiously, some of the laboratory specimens hooked their maxillipeds over their first antennae. In this position they seemed quite helpless and unable to get free. When the maxillipeds were released

by the investigator, the animal seemed quite healthy, but usually caught the maxillipeds again in a few hours.

Bathycalanus sp. There can be little doubt that these large red copepods from deep water must be carnivorous, although no food, plant or animal, was taken during the three weeks they were kept in the laboratory. The female whose respiration was measured was over 13 mm. long with antennae reaching over 2.5 cm. from tip to tip. In swimming, the movements were generally unhurried, almost deliberate, but when disturbed the animal dashed about the culture vessel in a frantic effort to escape, frequently sustained for some seconds.

Rhincalanus nasutus. This species survived well under laboratory conditions and ate any species of phytoplankton offered (*Skeletonema costatum, Thalassiosira decipiens, Rhizosolenia setigera*). One female lived for three months before being accidentally killed, during which time she matured and laid numerous fertile eggs. Attempts to raise the nauplii were unsuccessful.

Euchirella rostrata. These robust-appearing copepods did not survive particularly well in the laboratory although a few fecal pellets were produced when the animals were fed on *Skeletonema, Thalassiosira decipiens* and *Rhizosolenia.* All were dead within five weeks of capture, but during this period several females matured and laid. The eggs, which were a deep purple, were remarkable for their size relative to the animal which produced them. The lengths of the cephalothorax for the captive animals ranged from about 2.9 to 3.1 mm., while the eggs produced measured over 0.4 mm. in diameter. In contrast, *Rhincalanus nasutus,* size range 4.2–4.7 mm., laid eggs about 230 μ in diameter, and in the still larger *Calanus hyperboreus,* cephalothorax 5.5–6.0 mm., the eggs ranged from 190–210 μ. *Euchirella* laid only a few eggs at a time and they were very buoyant. Unfortunately none of the eggs developed.

The density of this animal in the adult stage was remarkably high in contrast to its eggs. The animals did not swim continuously in the laboratory containers and when swimming ceased, they sank rapidly to the bottom. The carapace seemed unusually sclerosed for so small an animal, being hard and smooth to the point of a dissecting needle. Their movements were exceedingly rapid and they leaped about vigorously when out of water. One individual traveled a measured distance of 20 cm. in a single leap from the shallow dish, containing water several millimeters deep, in which it was being examined. Although it was not demonstrated that *Euchirella rostrata* does prefer animal food, the generally poor feeding on phytoplankton, robust anatomy and prehensile head appendages make it virtually certain that the animal is largely carnivorous.

Other copepods. Only a few specimens of *Pleuromamma robusta* were taken in near-surface tows over the continental slope and no observations on the organisms in captivity were made. The structure of the mouth parts and general morphology would suggest that it is largely herbivorous (George Grice, personal communication).

No attempts were made to culture *Acartia clausi* at this time but earlier studies (Conover, 1956) leave little doubt that it is primarily a herbivore. However, two observations of considerable interest were made on the closely related species *A. tonsa.*

On one occasion, some *A. tonsa* taken from Woods Hole harbor were given as

food to a larger carnivorous copepod (*Paraeuchaeta norvegica*) in the company of some *Artemia* nauplii. During the experiment, an *Acartia* male was found which had firmly grasped with its head appendages an *Artemia* nauplius. When both animals were transferred to another dish for observation the male released the nauplius which was seen to have its abdomen almost totally eaten. The *Acartia* was given additional *Artemia* nauplii but died shortly thereafter without any further predation.

On another occasion, *A. tonsa* was observed in the act of feeding on a culture of large *Thalassiosira decipiens* (cells 70–85 μ in diameter). A female (cephalothorax length 0.87 mm.), lying ventral side up on the bottom of the dish, was seen to grasp single *Thalassiosira* cells with rapid movements of the maxillipeds, bringing them to the mouth region. Several times the individual cell could be seen poised on the edge of the labrum for an instant before it passed inside the animal without being broken or apparently damaged in any way. Once inside, the cells could be seen through the transparent carapace like beads on a string lined up along the foregut. The cells were carried posteriorly by a series of peristaltic movements during which they continued to be discrete, undamaged cells until quite suddenly they lost their distinct outline and seemed to fuse into a mass which soon became noticeably darker in color. The material was passed posteriorly and eventually extruded as a fecal pellet. The entire process took about 30–45 minutes, depending on which cell was timed. On examination the pellet was seen to contain only shattered frustules of *T. decipiens* and some unidentified organic matter.

Amphipods

Only two *Phronima* were taken during the program and one was dried after the respiration experiment. Despite their transparent, somewhat delicate appearance, the organisms were quite dense with a tough, sclerosed exoskeleton. The specimens studied here were found free-living in the plankton but the animal is frequently found "living" in an empty test of a salp. Most probably the organism eats the salp in whose test it is found, for it would seem poorly equipped for filter feeding.

Euthemisto compressa was found to produce an occasional fecal pellet when given phytoplankton (*Skeletonema*) but was obviously much more successful with animal food. For instance, between October 3 and October 6, 1958, a single female was observed to eat four harbor copepods and two zoeae, one nearly as large as itself. Gravid females were taken in the plankton on several occasions, and even the newly hatched young seemed carnivorous, swarming all over a piece of dead euphausid given them. *Hyperia galba* likewise is largely carnivorous and was observed to eat bits of mussel (*Mytilus edulis*), smashed snail (*Littorina littorea*) as well as living and dead copepods. This species is frequently associated with *Aurelia aurita* or other large medusae and may share the food captured by its larger host, but it can be a free-living member of the plankton community as well (Bigelow, 1925).

Both *Euthemisto* and *Hyperia* are quite dense, heavily sclerosed, and strong swimmers. Curiously, their carapaces are strongly hydrophobic and despite their density and obvious strength, they are very prone to become caught in the surface film.

Euphausids

Of all the oceanic organisms tried, the euphausids seemed to be the most difficult to keep in the laboratory. Specimens taken on August 19, 1958, were all dead by September 4, before anything could be ascertained about their food habits. On other occasions, *Thysanoessa*, *Meganyctiphanes*, and *Nematoscelis* have been observed to eat phytoplankton (*Skeletonema costatum*, *Thalassiosira fluviatilis*), but the rate of consumption would seem to be much too low to meet food requirements. These animals did not survive appreciably better than the first group.

Several workers have noted that euphausids consume a variety of foods. *Nyctiphanes couchii*, a neritic species, eats diatoms and organic detritus predominantly but also catches *Sagitta*, smaller crustaceans, and is cannibalistic in the laboratory (Lebour, 1925). Similarly, *Meganyctiphanes norvegica* consumed plant detritus when it was present in the water, but also fed on *Calanus finmarchicus*, *Paraeuchaeta norvegica* and smaller copepods (MacDonald, 1927). Very probably most euphausids are omnivorous, but it is difficult to explain their extreme sensitivity to deficiencies of the laboratory environment.

Respiration in Relation to Size of Planktonic Organism

It is generally believed that the respiratory rate of poikilothermal animals is related to some power of body weight by the expression

$$R = kW^x \qquad (1)$$

where R is the volume of oxygen consumed, W the body weight, k a constant for a given set of conditions, and x is the exponent, generally between 0.66 and 1.00. When oxygen consumption is plotted against weight on log log paper the data should give a straight line with a regression coefficient equivalent to x in equation (1).

Raymont and Gauld (1951) obtained a regression coefficient of 2.19 (or 2.30 with a single aberrant value removed) when log respiration was plotted against log length of the cephalothorax for four species of marine copepods ranging in length over a size range of nearly an order of magnitude. If it is assumed that weight varies as the cube of the length, then the coefficient obtained by Raymont and Gauld becomes 0.73 (or 0.77) in the form of equation (1).

In the case of nine species of small neritic copepods, Conover (1959) computed an overall regression coefficient of 0.86 for log respiration against log dry weight. For these copepods with a total size range considerably less than an order of magnitude, weight was found to vary as the power 3.17 of cephalothorax length.

The range of variation in weight of the organisms included in the current investigation is nearly four orders of magnitude and the variation in respiratory rate per organism is likewise considerable (Table I). A log log plot of respiration against weight would be expected to give a straight line relationship with a positive regression coefficient. However, if the respiration rate is first divided by the weight of the animal, the log log plot of this value R' against weight W should yield a negative regression coefficient. Of the two methods, the second shows more clearly the decrease in metabolic rate with increasing size, and its use should save a step in the calculation of energy flow and production rates.

The least squares regression on double logarithmic coordinates of the respiratory rates as μl. oxygen/mg. dry weight and day plotted against dry weight in μg., excluding only the values for *Calanus finmarchicus* at 18.5° C. and those for *Pleuromamma robusta*, gives the equation

$$\log R' = -0.35 \log W' + 2.2888. \quad (2)$$

In exponential form equation (2) becomes

$$R' = 194\ W'^{-0.35}. \quad (3)$$

For comparative purposes, equation (3) may be converted to the form of equation (1) by replacing R' with its equivalent R/W',

$$R = 194\ W'^{0.65}. \quad (4)$$

It can be readily seen that the exponential constant in (4) is decidedly lower than that observed by Conover (1959), and also is lower than the probable exponent computed from Raymont and Gauld (1951). Weymouth *et al.* (1944) obtained a coefficient of 0.798 for *Pugettia producta* and Vinberg (1950) recorded 0.81 for

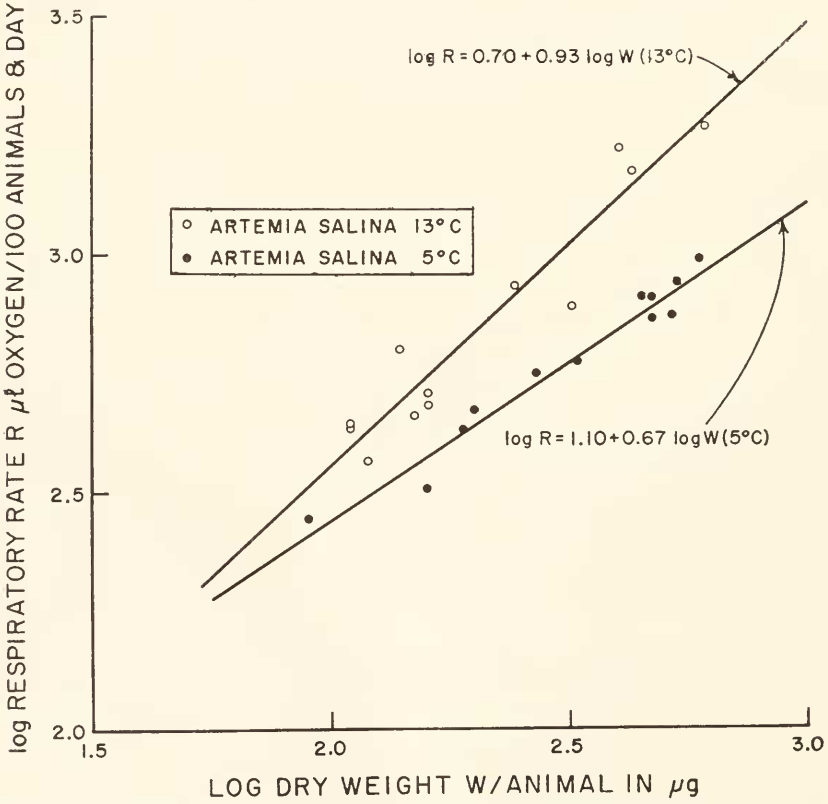

FIGURE 1. Regression lines for *Artemia salina*, showing log respiration in μl. O_2 animal and day plotted against log dry weight at 5° and 13° C.

TABLE II

Analysis of variance for regression of log respiration against log dry weight at two temperatures for Artemia salina

Null hypothesis: That there is no difference in regression coefficients for log respiration against log weight measured at 5° and 13° C.

Sources of variation	Degrees of freedom	Sums of squares	Mean square	Variance ratio
5° C. Linear relation	1	0.319323	0.319323	173.73
Error about line	10	0.018383	0.001838	—
13° C. Linear relation	1	0.625688	0.625688	103.16
Error about line	10	0.060651	0.006065	—
Combined slope	1	0.921432	0.921432	233.17
Between regression coefficients	1	0.023579	0.023579	5.97
Combined error	20	0.079034	0.003952	

Variance ratio F for difference between regression coefficients = 5.97; $F_{0.975}$ (1, 20) = 5.87. Since F (1, 20) >5.87, reject null hypothesis.

Gammarus lacustris. Assuming that surface area is proportional to the square of length and that weight is proportional to the cube of length, von Bertalanffy (1951) suggested that an exponential constant of 0.667 indicates direct proportionality of metabolism to the relative surface area of the organisms. The exponential constant from equation (4) might, therefore, suggest that the surface rule applied in the case of the zooplankton investigated in the current study but not for the earlier work. However, there is also the possibility that the lower coefficient of proportionality observed here may result from the different temperature at which the experiments were run. In contrast with the temperatures of 4–8° C. used in the present work, Raymont and Gauld (1951) performed their experiments at about 17° C. and Conover (1959) used 20° as the experimental temperature. Vinberg (1950) and Weymouth *et al.* (1944) also used temperatures appreciably higher than those in the present work.

To test the hypothesis that the temperature at which a series of experiments is performed with different sized organisms might affect the proportionality of respiratory rate to size, an initial experiment with three species of calanoid copepods, ranging in weight from 0.017 to 5.45 mg., was set up at two temperatures, 5° and 13° C.; however, the scatter around the least squares regression lines was too great to permit disproof of the null hypothesis that there was no difference in the log log regression coefficient of respiration against weight at the chosen temperatures. A second experiment at the same two temperatures was then performed with a single species, *Artemia salina*, which can be cultured in the laboratory so as to supply a number of different size classes. The least square regression lines for log respiration against log weight for *Artemia* at 5 and 13° C. are shown in Figure 1. The regression coefficients, 0.67 at 5° C. and 0.93 at 13° C., can be demonstrated to be statistically different at $P = 0.025$ (Table II). According to von Bertalanffy (1951) the two regression coefficients obtained here for the same animal would be indicative of two very different metabolic types.

So long as the Q_{10} for any temperature change is the same for an animal over its entire size range, the regression of respiration against weight should give the same coefficient of proportionality regardless of the experimental temperature. In this regard, Rao and Bullock (1954) reviewed data from several sources, and concluded that the Q_{10} of various measures of activity commonly increases with increasing size over the range of ordinary physiological temperatures, although there were several cases in which the trend was reversed. *Artemia* was not one of the animals considered by Rao and Bullock, but the present data would seem to suggest that this animal does have a Q_{10} which varies with size.

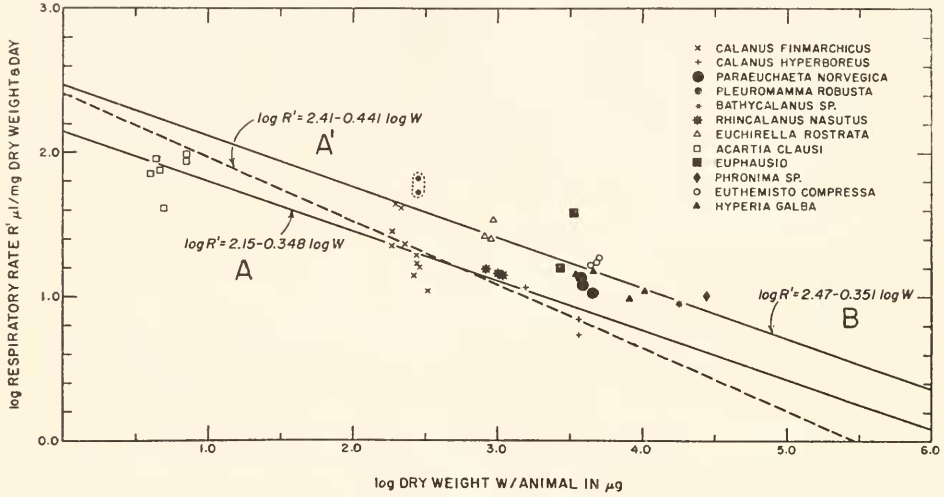

FIGURE 2. Scatter diagram and regression lines showing the relation between log respiration in μl. O_2/mg. dry weight and day and log dry weight in μg. Line A is fitted to data for suspected herbivores. Line A' is fitted to data for herbivores, omitting values for *Acartia clausi*. Line B is fitted to data for suspected carnivores. See text for further explanation.

In the case of studies involving several different organisms taken from nature, there is the additional complexity of species differences in Q_{10}. Rao and Bullock (1954) also showed that the habitat temperatures of the animal prior to examination could affect Q_{10}. In this regard, Berg and Ockelmann (1959) observed a seasonal shift in the size-respiration relationship for the fresh-water snail *Lymnaea palustris*. Other factors, such as nutritional status, reproductive activity or some endogenous rhythm, might lead to increased variability in the observations. The resultant of one or several factors of the sort described here might be to increase or decrease the spread of values at one end of the temperature scale while having the opposite effect at the other end, regardless of the size of the animals being studied. Both the slope of the regression line and the scatter of points around it would be affected.

Respiration in Relation to Food Habits

It was noted early in the study that *Calanus hyperboreus* and *Paraeuchaeta norvegica* taken in the same tow and studied under the same conditions had different

respiratory rates despite their similarity in size and weight (see Table I). Both animals were kept in the laboratory for a lengthy period, and it became obvious that one, *Calanus hyperboreus*, was principally herbivorous while the other was entirely carnivorous. Raymont (1959) found that *Tortanus discaudatus*, also believed to be a carnivore, appeared to have a higher metabolic rate in relation to its body size than other copepods inhabiting the same type of environment.

In Figure 2 the respiratory rate at low temperatures for all the animals studied has been plotted against their weight on double log paper. On examination of the scatter diagram it seemed that the suspected carnivores in general had higher rates than the known herbivores. To test this hypothesis, separate regression lines were

TABLE III

Analysis of covariance for respiratory rates of herbivores (Acartia clausi *included) and non-herbivores*

Null hypothesis: That there is no difference in the respiration rate per mg. of dry body weight for herbivorous and non-herbivorous zooplankton

Sources of variation	Degrees of freedom	Sums of squares for respiration	Sums of products for respiration and weight	Sums of squares for weights	Errors of Estimate		
					Sums of squares	Degrees of freedom	Mean square
Total	38	3.76580	−10.74861	43.19223	1.09095	37	
Between animals having different food habits	1	0.38487	−2.80085	20.38336			
Within each type	37	0.38093	−7.94776	22.80887	0.61153	36	0.01699
For test of significance of mean respiration with effect of weight removed					0.47942	1	0.47942

Variance ratio $F = \frac{0.47942}{0.01699} = 28.2$; $F_{0.999}(1, 40) = 12.61$. Since $F(1, 36) > 12.61$, reject null hypothesis.

fitted to the data for the herbivores, *Calanus finmarchicus, C. hyperboreus, Rhincalanus nasutus*, and *Acartia clausi* (line A), and a second line fitted for the suspected carnivores, *Paraeuchaeta norvegica, Bathycalanus, Euchirella rostrata, Phronima, Euthemisto compressa, Hyperia galba*, and the euphausids (B). For the herbivores an additional regression line was also computed, omitting the data for *Acartia* since it had been acquired originally for different reasons (A′). Obviously the slope of the regression lines for the herbivores (including *Acartia* data) and the non-herbivores is not significantly different (0.348 and 0.350, respectively). With the *Acartia* data omitted the slope of the regression line fitted to the herbivore data becomes 0.441, but it can be shown statistically (Student's t test) that the slopes are still not significantly different.

To test the null hypothesis that there is no difference between the regression lines for herbivores and non-herbivores, an analysis of covariance was employed as shown in Table III. Since the slope for the herbivorous animals was not affected

by removing the *Acartia* data, it was decided to include this in the overall analysis. It is one of the advantages of covariance analysis that differences between groups of measurements can be tested in a single operation without the effect of other measurements that would normally complicate the interpretation. Thus, errors of estimate are calculated from the sums of squares and sums of products in such a way that the variance ratio tests only the respiratory rates after adjustment to remove the effect of the variable weight. Since the F test suggests that the distribution of respiration rates in relation to feeding type observed here would occur by chance much less than one time in a thousand, clearly the reason for the distribution bears some consideration.

Certain of the non-herbivorous zooplankton organisms studied were observed to be quite dense, with a hardened exoskeleton. Thus, organisms such as *Euchirella rostrata, Euthemisto compressa,* and *Hyperia galba* are presumably carrying around a considerable weight of inert organic material. More muscle protein, also quite dense, and more energy would be required to maintain the organism in the water column against its negative buoyancy.

There is little doubt that many herbivorous copepods also carry a high portion of their body weight as inert organic material, but in this case the substance may be oil with a positive buoyancy. In the case of the large *Calanus hyperboreus,* copepods of approximately the same external dimensions may differ in dry weight by several hundred per cent because of differences in the amount of stored oil.

It is also probable that a carnivorous animal is normally more active than an herbivorous one, regardless of their basal metabolic rates. The predator has to move about actively in search of the prey and then must overcome the natural reluctance of the prey to be caught by using its greater physical strength and swiftness. On the other hand, the prey organism in this association is more often than not the herbivorous copepod which can feed while it swims with a more or less continuous expenditure of a smaller amount of energy, since its food has at best extremely feeble power of escape.

Finally the possibility remains that a real difference could exist in the form of the organic matter oxidized by the herbivore and non-herbivore. Thus, an organism which burns carbohydrate exclusively would use decidedly less oxygen per unit of carbon oxidized than one which metabolizes oxygen-poor fats.

Before leaving the subject of respiration, a few remarks should be made concerning *Pleuromamma robusta* and its somewhat enigmatic position metabolically. As remarked earlier, it would appear that this species belongs in the herbivorous group, but so far as its respiration is concerned the organism would seem to be more closely allied to the non-herbivores. Clearly, with only two points on the graph it is not certain that any real difference exists between this and other herbivorous forms so far as respiration is concerned, and yet it remains possible that the very high metabolic rate observed for this form may be in some way related to the fact that it has a powerful bioluminescent organ. The species should certainly be given further attention.

Discussion

There is a persistent tendency for the biologist working with the most complex of organized systems to seek a simple solution or approximation which holds for the majority of cases. Thus certain scientific "laws" as $Q_{10} = 2$, metabolism equals

a constant times weight to some power between 0.7 and 0.8, weight equals cube of length, and so on have come into common usage in environmental studies. Most of these "laws" had their origin in laboratory studies on mammals and they need re-examination before being applied to many ecological situations. It would be a great advantage to the biological oceanographer to have a single expression which would predict the metabolism of a population of organisms with a given size distribution under any temperature conditions, but as more data become available the evidence would suggest that such a prediction equation, if it is ever formulated, will give a high-speed computer a good workout.

The relationship between metabolism and size in the warm-blooded organisms on the average has the form

$$M = 70W^{0.74} \text{ cal./day}, \tag{5}$$

but as Kleiber (1947) admits, the basis for this relationship is not really understood for the best known group of mammals. In the case of warm-blooded organisms metabolism is usually measured at or near the same temperature and the necessity to maintain this temperature against external environmental temperatures often very different would seem to give some importance to the relative surface area across which heat would be lost or gained.

In the sea, among the cold-blooded organisms there is tremendous variety in body form, biochemical mechanism and chemical composition. The surface of the marine organism is important for several reasons. Besides heat, nutrient substances, excretory substances, and gases pass back and forth across body membranes, and the frictional resistance of the surface area with the surrounding medium is critical for all organisms which move from place to place, whether they swim or are carried by their environment. It would seem very coincidental indeed should all the myriad forms of life be governed by a law derived from the warm-blooded organisms.

Among the marine invertebrates these problems have been examined in detail only for the Crustacea, and here it is true that there are relationships between metabolism and size very similar to those derived for homeothermal organisms. However, the effect of environmental temperatures on these relationships has not been given much prior consideration.

That other factors besides size and the direct effect of temperature influence respiratory rates of zooplankton forms has also been demonstrated recently. Conover (1956) observed a possible seasonal adaptation to the changing temperature regime for *Acartia clausi* and *A. tonsa*. Subsequently Conover (1959) and Marshall and Orr (1958) demonstrated seasonal differences in the respiration rate of several neritic species. Conover (1959) also demonstrated a significant difference between the respiratory rate of *Acartia clausi* in Long Island Sound and in Southampton Water. It can be seen from Table I of this study that *Calanus finmarchicus* had a decidedly higher respiratory rate on Georges Bank than in the Gulf of Maine. In this case, the populations are separated by not more than a hundred miles of water. To this list can now be added the difference in metabolism between organisms belonging to the same community but differing in their position within the food chain.

As a final note of complexity to the already confused picture of metabolic rela-

tionships for the planktonic organisms, it must be emphasized that even though reliable data were available for respiration per unit mass for a group of organisms, conversion of this information to food requirements or energy flow might introduce an appreciable error, due to insufficient knowledge regarding the nature of the food substance oxidized. It is well known that an animal requires more oxygen to oxidize fat than to oxidize carbohydrate. Although more energy is produced per volume of oxygen used in the case of carbohydrate metabolism, there is also more energy available per gram of fat than per gram of carbohydrate. Raymont and Conover (unpublished data) observed that several zooplankton organisms oxidized carbon in some form at a rate of at least ten times greater than changes in their carbohydrate reserves would predict. For instance, in the case of *Calanus hyperboreus*, the respiration rate was equivalent to an oxidation of 10 to 20 μg. of carbohydrate per day, an amount somewhat greater than the total carbohydrate content of the animals, and yet there was no detectable change in the total sugars.

It is becoming increasingly popular among environmental biologists to think of production as a single dynamic process which can be made to conform to some idealized mathematical model. Such an approach has had useful application, for instance in the North Sea pelagic fishery studies by Cushing (1955, 1959). Yet, as Steele (1960) points out, herring eat *Calanus* but they do not eat salps, even though each has a similar position in the food chain. Perhaps it is fortunate that salps are not particularly abundant in the North Sea! In any event, there would seem to be a good argument in favor of an increased emphasis on certain qualitative aspects of energy dynamics and food relations in the marine environment as a supplement to the purely quantitative approach.

Summary

1. The respiration rate of twelve species of zooplankton, the majority from oceanic waters and from depths greater than 100 meters, has been measured at temperatures close to that of their environment (4–8° C.). In most cases healthy specimens were brought to the laboratory and their food habits and behavior studied.

2. The following species seemed largely herbivorous: *Calanus finmarchicus, C. hyperboreus,* and *Rhincalanus nasutus.*

3. The copepod *Paraeuchaeta norvegica,* and the amphipods *Euthemisto compressa* and *Hyperia galba* all took animal food readily. *Bathycalanus* sp., *Euchirella rostrata* and the euphausids also are believed to be at least partially carnivorous although they demonstrated little or no feeding.

4. The animals studied had a total range in dry weight of nearly four orders of magnitude. When log respiration was correlated with log weight, a positive linear regression coefficient of 0.65 was obtained. This value, which is lower than most previously determined regression coefficients relating size and metabolism in the Crustacea, may result from the lower temperatures used in these experiments compared with those used in the earlier work.

5. As confirmatory evidence, size and metabolism were related by a coefficient of 0.67 at 5° and 0.93 at 13° in the case of *Artemia salina.*

6. Those zooplankton animals which seemed to be largely carnivorous on the basis of the behavioral studies had a significantly higher respiratory rate than those which seemed to be predominantly herbivorous.

7. Some of the possible explanations and ecological implications of the above-mentioned observations are discussed.

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